

SUSCEPTIBILITY GRADIENTS IN THE HAIRS OF CERTAIN MARINE ALGÆ.

C. M. CHILD,

WITH FIVE FIGURES.

The colorless hairs or capillary branches so common on the red and the brown algæ are in many cases beautiful objects for the study of the axial susceptibility gradients. A few data obtained during the summer of 1915 at Woods Hole have already been published (Child, '16a). The present paper records the result of further investigation during the summer of 1916 on the physiological polarity of these hairs and includes data on additional species, experimental results on modification of the gradients which answer certain questions raised by the earlier work, and also a correction of the earlier observations concerning one species.

Thus far hairs of the following three types have been examined:

Unbranched unicellular hairs, *Ceramium*, *Chondrus*, *Agardhiella*. The hair is a very slender and delicate outgrowth, sometimes reaching a length of several millimeters, but unicellular.

Unbranched multicellular hairs with basal vegetative tip, *Fucus*, *Castagnea*.

Branched, multicellular hairs with apical vegetative tip, *Chondria*, *Polysiphonia*, *Griffithsia*.

Although this grouping of species according to the form of the hairs does not represent the taxonomic order, it seems the most satisfactory for present purposes since only the hairs are to be considered. In most species examined the hairs are so extremely sensitive that conclusions concerning the existence of a gradient and its direction can be safely drawn only from plants in the best possible physiological condition, collected with the minimum of handling and examined at most within a few hours after collection. Within the first few days in the laboratory, even in running water, the hairs usually die and often drop off, although

other parts of the plant may remain alive and apparently in good condition.

In the earlier observations on the hairs (Child, '16) the extreme sensitiveness and rapidity with which alterations in the gradients may occur was not fully recognized, consequently some of the statements made at that time require correction.

Since the hairs are without pigment and their protoplasm is in most cases almost entirely devoid of visible structure, except under high powers, in the living condition a susceptibility gradient can be made visible only by staining with neutral red or some other vital dye and then killing with the proper concentration of some reagent. As killing agents neutral red, KCN and HgCl_2 were chiefly used.

UNBRANCHED UNICELLULAR HAIRS.

Ceramium rubrum constituted the chief material for the study of hairs of this kind. In the earlier paper it was stated that "in the long full-grown hairs the susceptibility gradient is distinctly acropetal while in those which are apparently still growing it is basipetal" (Child, '16, p. 104). The later observations indicate that the normal or primary gradient is basipetal in all hairs, but that it may readily undergo reversal. In the observations of 1915 the hairs were first stained with neutral red and then killed in KCN $m/100$. In 1916 it was found that when neutral red was used both as staining and killing agent the more susceptible hairs which died during the first 1 to 2 hours showed almost without exception a basipetal gradient, *i. e.*, death began apically and proceeded basipetally, while among many less susceptible hairs which died later basipetal gradients were much less frequent, many hairs showed no definite death gradient, and acropetal gradients were often observed. Apparently if the neutral red kills the hair rapidly enough the death gradient is basipetal, but where death occurs only after a longer time the original gradient may be obliterated or even reversed. In short the neutral red may obliterate or reverse the original gradient in susceptibility to itself.

Hairs stained for a few moments in neutral red and then killed in KCN usually show a basipetal gradient, but when stained for

an hour or more and killed in KCN the frequency of basipetal gradients is lower and that of acropetal gradients higher, *i. e.*, the neutral red tends to reverse the susceptibility gradient at least to some other agents as well as to itself. Discussion of these and other cases of reversal is postponed to the final section.

Ceramium rubrum is in general highly resistant to depressing conditions and the hairs are much less sensitive than those of many other forms. It has been observed, however, that in plants kept in the laboratory for several days the hairs are usually less susceptible, and acropetal gradients are more frequent than in fresh specimens.

The visible death-changes in these hairs are very similar to those in other cells (Child, '16a, '16b). A slight basipetal staining gradient may or may not be visible. Before the aggregation and decoloration of the protoplasm the usual change in color to deeper red occurs, and this color change commonly shows a basipetal gradient where the death gradient is basipetal. Often death is preceded by plasmolysis which proceeds in the same direction as death and not infrequently a more or less regular gradient in length of the plasmolyzed portions appears, the most apical portion being shortest and the length increasing basipetally (Fig. 1). In other cases the protoplasm may separate into only two or three portions, and death may also occur without preceding plasmolysis. Instead of separating into distinct portions the protoplasm often undergoes a plasmolytic contraction, as a single mass, retracting slightly as a rule from the apical end and basally from one third to two thirds of the hair length. Both the gradient in length of plasmolyzed portions and the difference in apical and basal retraction indicate a graded difference in protoplasmic condition along the axis.

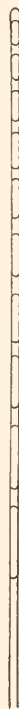


FIG. 1.

The final change in the protoplasm is the apparent collapse of the protoplast or its separate portions and the aggregation into small masses stained almost black. Where the basipetal gradient is well marked this change begins apically and can be followed basipetally along the hair. Where the gradient is obliterated it may begin at almost any level, or at several levels, or may be

simultaneous throughout the length, and where the gradient is acropetal it begins at the basal end of the protoplasm and proceeds acropetally. The deep stain of the masses scattered along the cell rapidly fades and the hair presents almost the appearance of the normal hair, but a careful examination with proper illumination shows the aggregated protoplasmic masses which are still transparent and are visible only because of their refractive index.

The hairs of *Chondrus crispus* and *Agardhiella tenera* are similar in structure to those of *Ceramium* and the few incidental observations made on these species indicate that they behave in essentially the same way. The hairs on freshly collected plants in good condition usually show a basipetal gradient. Most of the hairs die during the first two or three days in the laboratory and acropetal gradients with decreased susceptibility are often observed before they die. Plasmolytic separation or basal retraction of the protoplasm also often precedes death and the final changes are similar to those in *Ceramium*. In the hairs of *Ceramium* and *Agardhiella* the basal retraction of protoplasm often occurs merely as the result of laboratory conditions and before death the entire protoplasm of the hairs may be contracted into a mass one fifth or less of the length of the hair, lying near the apical end and as might be expected, staining much more deeply than in the normal condition. Similar changes probably occur in the hairs of *Chondrus* but have not as yet been looked for.

UNBRANCHED MULTICELLULAR HAIRS.

Hairs of this kind consist of a single series of cells (Figs. 2 and 3), and in the only two species examined, *Fucus vesiculosus* and *Castagnea tuberculosa*, the vegetative point of the hair is at its attached basal instead of at the free apical end. Because of this fact observations on the susceptibility gradients of these hairs are of particular interest.

In *Fucus* the hairs develop from the inner walls of flask-shaped cavities on the thallus, and later from the walls of the conceptacles. The hairs reach the exterior through the narrow neck of the cavity and form dense tufts, often several millimeters long. As noted above, the growing point of the hair is basal, *i. e.*, next

to the wall of the cavity and is therefore not visible in intact specimens, but the fact that the length of the cells increases from the most basal region visible toward the free end suggests that cell division is basal instead of apical. Fig. 2 shows a hair of *Fucus*, the basal concealed portion being diagrammatically indicated in dotted lines.

In freshly collected plants the hairs are extremely sensitive and even in dilute neutral red death begins within a minute or two, often before the preparation can be placed under the microscope, and in a few minutes the whole hair is dead. In such hairs the gradient is acropetal, *i. e.*, the basal region of the hair is the region of highest susceptibility. The acropetal gradient is very distinct and uniform in the progress of death from cell to cell and in the longer, older cells nearer the free end the acropetal intracellular gradient can usually be seen if death is not too rapid. In the shorter, younger cells an intracellular gradient is usually not visible in the concentrations ordinarily used for killing. The high susceptibility of the hairs makes it impossible to stain with neutral red and then use other agents for killing.

At the time of my first observations on the susceptibility of these hairs I was entirely ignorant of the fact that they grew from a basal instead of an apical vegetative point or "growing tip," but the presence of very distinct acropetal instead of basipetal gradients in all hairs of freshly collected plants constituted practically conclusive evidence for the existence of a basal vegetative region and examination of the cellular structure of the hair and reference to the literature confirmed the conclusion. In this case then the direction of the gradient made possible the immediate recognition of the rather unusual growth form.

In freshly collected plants in good condition and very carefully handled, particularly in small young thalli, there may be practically no irregularities or exceptions to the regular acropetal course of death in the hairs of the whole thallus. After a few hours in the laboratory, however, or after exposure to unfavorable conditions, *e. g.*, partial drying at low tide, the change in the condition of these hairs is very striking.

FIG. 2.

The most susceptible basal region is almost invariably dead, the dead region usually including the two or three most basal cells visible, and the gradient is usually completely reversed in the more distal regions of the hair. Instead of being practically instantaneous, as in the hair when in good condition, staining with neutral red occurs very slowly, and a basipetal staining gradient appears, *i. e.*, the most distal cell stains most rapidly and the rate decreases basipetally from cell to cell. The same basipetal gradient appears in the course of death.

In these hairs with reversed gradient the susceptibility of the most distal region is not much altered; this is the least susceptible region, the last to die in the normal hair and the most susceptible in the hair with reversed gradient, but its susceptibility is very much the same in the two cases. The more basal the level, *i. e.*, the higher the original susceptibility, the greater the decrease in susceptibility afterward, until in the more basal regions the cells which were originally most susceptible of all are dead.

The cells next to these dead basal cells show the structure of dying cells as soon as they begin to stain, *i. e.*, masses of aggregated protoplasm which stain almost black are already present, but include only a part of the protoplasm, and the remainder stains diffusely in the usual way. When the death of such cells is finally completed the remainder of the protoplasm is aggregated into deeply staining masses in the usual way and the diffuse stain disappears. In these cases the death-changes in a single cell may extend over hours. It is a fact of considerable interest that the cellular death-changes resulting from unfavorable conditions in the laboratory or in nature are the same in appearance as those occurring in neutral red and other killing agents.

The very great change in susceptibility in some cells of the hair after reversal of the gradient is indicated by the fact that the cells of the more basal levels which die in one or two minutes in neutral red when the hair is in good condition may survive for twenty-four hours in neutral red after reversal.

What happens in such reversal is apparently this. The hair is very sensitive and under depressing environmental conditions the basal, most susceptible region dies as it does in solutions of killing agents in the laboratory. Next to this region are cells,

originally somewhat less susceptible, and these are "almost" or "partly" killed and their metabolic rate so decreased and protoplasmic condition so altered that they become very insusceptible in killing agents. Still farther distally the effect of the altered conditions is less marked until finally little or no change occurs in the most distal cell. If we now subject a hair altered in this way to the action of a killing agent such as neutral red, KCN, etc., we find that the altered condition appears in the altered susceptibility to the killing agent. The fact that the changes produced by some external agent or complex appear as altered or reversed susceptibility to another is of interest and brings up the question whether the action of the two agents is additive or not. But whatever the nature of the processes, the fact of reversal is sufficiently evident, and, as in other cases, supplements the direct evidence for the existence of a dynamic gradient.

Castagnea tuberculosa bears very fragile unbranched multicellular hairs, which like those of *Fucus* develop from a basal vegetative point concealed below the surface of the thallus. Fig. 3 shows the general appearance of the hair, the concealed basal portion being diagrammatically indicated in dotted lines. In my earlier paper (Child, '16a, p. 101) I stated that the gradient in these hairs is in general basipetal, but with frequent irregularities, and the earlier observations of 1916 also showed in general a basipetal gradient. In all these cases, however, the plants used had been in the laboratory a day or more and further investigation on fresh material showed that the gradient is primarily acropetal, but very readily undergoes more or less complete reversal as in *Fucus*. In fact, even in freshly collected material apparently in good condition, but with long well-developed hairs, reversal has been observed in many cases.

At the time of the earlier observations I did not realize how readily reversal of the gradient might occur nor was I aware that the vegetative point in these hairs is basal and not apical, and when a well-marked basipetal gradient was found as a rule in plants which had been in the laboratory a day or two, I failed to realize the necessity of checking up the results on perfectly fresh



FIG. 3.

material. The cells of the *Castagnea* hair attain their full size very near the basal end, so that in that portion of the hair visible in the living plant the cells are all of practically the same diameter and length and it is difficult or impossible to determine the position of the growing point from a gradation in cell size. This case shows how readily incorrect conclusions may be drawn where the material is not in perfect condition. These hairs, like those of *Fucus*, are very sensitive and the gradient undergoes reversal very readily, but there can be no doubt that it is primarily acropetal, not basipetal, as stated in my earlier paper. The hairs are so fragile that they are readily broken or injured mechanically and at least many of the irregularities are due to such injuries.

BRANCHED MULTICELLULAR HAIRS.

Among hairs of this kind those of *Chondria* have served as the chief material, but the hairs of *Polysiphonia* and *Griffithsia* have also been examined. The hair of *Chondria* develops by repeated apical dichotomy (Fig. 4), and since growth is primarily apical a basipetal death gradient is to be expected. In 1915 hairs of this species were examined by first staining deeply with neutral red and then killing in KCN and the gradient from cell to cell was found to be distinctly basipetal while within single cells an acropetal gradient was almost invariably observed (Child' 16a, pp. 105-106). Since these observations were made during the last days of my stay at Woods Hole in 1915 there was no opportunity to repeat the observations with fresh material until the following year. As regards the acropetal cell gradient the results of 1916 are as follows: When the hairs are killed in a high concentration of neutral red alone (*e. g.*, before precipitation in sea-water) both hair gradient and intracellular gradient are very uniformly basipetal. Similarly when the hairs are killed in some other agent (KCN $m/1000 - m/100$, $HgCl_2$ $m/50000$) to which a few drops of neutral red have been added to stain the hairs slightly and so make the death-changes clearly visible, both hair-gradient and cell-gradient are basipetal. On the other hand, when the hairs are first deeply stained with neutral red and then killed in KCN or some other agent, the method used in 1915, the

hair gradient is basipetal but the cell gradient is very generally acropetal.

Evidently the acropetal cell-gradient observed in 1915 is not a natural condition but represents a reversal of the cell gradient by neutral red or by other conditions, and this appears as a reversed susceptibility gradient to KCN or HgCl_2 . These hairs take up neutral red rapidly and stain very deeply, and the axial differences in susceptibility to neutral red within the elongated

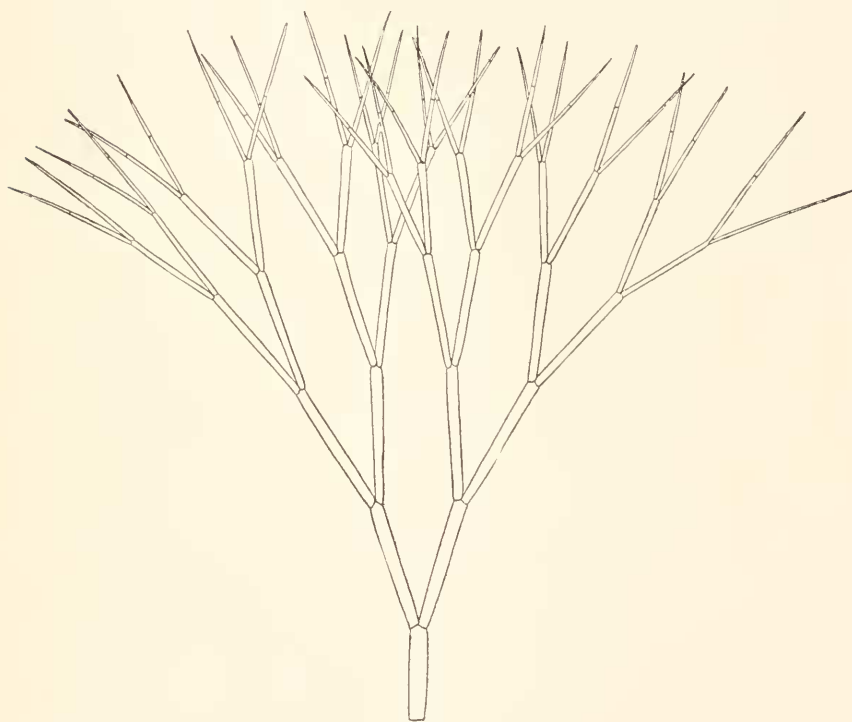


FIG. 4.

cell are sufficient to bring about reversal of the susceptibility gradient after a time. If death occurs early the reversal does not appear, but if the concentration of neutral red is low enough to allow survival for two or three hours in the solution, reversals of the cell gradient begin to appear.

Further observations showed that after two or three days in the laboratory the intracellular gradient was frequently reversed,

particularly in the more basal cells of the older hairs. Similarly in plants found detached reversed intracellular gradients were often observed. Such plants torn loose by the waves and washed into shallow water may be exposed to depressing conditions of temperature, light, or partial drying at low tide. There is of course no way of determining what or how extreme these conditions have been in a particular case but the fact that reversed intracellular gradients appear frequently in the hairs of such plants but are not present in material which so far as can be determined is in the best physiological condition, together with the data on experimental reversal, indicate clearly enough that such reversals are the result of depressing or toxic factors.

Whatever the processes involved in such reversals, they, like other reversals described in this and an earlier paper (Child '16b), are dependent on the preëxistence of a basipetal susceptibility gradient in the cell, and they represent the differential action of external factors within certain limits of concentration or intensity upon this gradient. The difference in susceptibility between different cells, even two adjoining cells, is usually greater than the differences between the two ends of a single cell, and the difference between apical and basal cells of a hair is of course very much greater than any intracellular differences. The persistence of the hair gradient with reversal of the intracellular gradient indicates merely that the relations between the lesser differences in susceptibility are more readily reversed than those between the greater differences.

The establishment of the fact that the acropetal intracellular gradient is a reversal of the original gradient at once raises the question whether the gradient of the hair as a whole can be reversed. Various attempts at such reversal have been made with some success, particularly in the younger hairs, but in the full-grown hairs the axial differences in susceptibility are so great that complete reversal has not as yet been induced and is perhaps impossible.

In *Chondria* the hairs occur in large numbers near the apical ends of branches of the thallus, and in cases where extensive hair-development occurs the hairs appear macroscopically as white tufts covering the branch tips. A well-developed tuft of

this kind is made up of hairs of very different stages of development and physiological age, the most basal hairs being in general the earliest developed and so the largest and the oldest, while the most apical are the latest, smallest and youngest, with intermediate stages between the two extremes. The differences in physiological age in such a group are beautifully shown by the differences in susceptibility, the youngest hairs being most susceptible, the oldest least, with a general gradation in susceptibility between. These age differences appear even in the susceptibility of the apical cells, those cells of the young hair being somewhat more susceptible than those of the old, but this difference between apical cells of young and old hairs is much less than that between the more basal cells. In KCN $m/1000$ for example, apical cells of the youngest hairs die almost at once, those of the oldest hairs after 1-5 minutes, but in the youngest hairs death is complete all the way to the basal cell in 10-15 minutes while in the oldest the most basal cells may live for 2-3 hours. In the young hair the basal cells have not yet had time to become old, while in the old hair the basal cells have reached an advanced stage of physiological senescence, and in the apical cells senescence has progressed to a greater or less extent, but has been counterbalanced to some extent by the periodic rejuvenescence accompanying cell reproduction (Child, '15a, Chap. X.). These susceptibility relations between the older and younger hairs of a single group and between apical and basal regions of a single hair constitute a most beautiful and striking example of the course of senescence in plant axes.

The attempts to reverse the whole hair gradient were made with tufts of this sort, consisting often of hundreds of hairs of all ages and stages of development, their attachment to the branch from which they arose being of course undisturbed. In this way it was possible to observe the difference in the reaction of old and young hairs to particular experimental conditions.

The result of a few experiments along this line which serve merely to suggest the possibilities, are briefly stated. Exposure to temperatures of 30°-35° C. for three or four hours killed the youngest hairs completely or all but one or two basal cells, almost without exception. The hairs of medium age and susceptibility,

however, showed a high percentage of complete reversals of the gradient, death beginning basally and proceeding apically, the apical cell being the last to die. In some other hairs of this group partial reversal of the hair gradient occurred, *i. e.*, the apical cell died first, and one or two cells below it in basipetal order, while in more basal regions the progress of death was acropetal, both from cell to cell and within the cells. In the oldest hairs the hair gradient was usually basipetal, in the apical third or half of the hair, *i. e.*, for a length of three to five cells, although the intracellular gradients were often acropetal, particularly in the more basal cells of this region. In the basal half or two thirds of such hairs there was usually more or less reversal of the hair gradient, the basal cell dying first, and one, two or even three cells apical to it dying in acropetal order. The intracellular gradients were very commonly acropetal in this region. In short, by this exposure to high temperature the most susceptible hairs were entirely killed, those of medium susceptibility showed complete or nearly complete reversal and the oldest showed more or less reversal in the basal regions. The susceptibility of all living hairs and cells was of course much lower than that of corresponding hairs or cells in good condition tested at the same temperature, and the susceptibility of the hairs of medium age in which the gradient had been reversed was usually as low as, or even lower than that of the oldest hairs. The experiment shows a gradient in injury by the high temperature both in the single hair and corresponding to age-differences in the tuft, the degree of injury varying in general with the normal susceptibility of different hairs and different levels.

With short periods of exposure complete reversal was obtained in the youngest hairs in many cases, partial basal reversal in those of medium age and in some of the oldest hairs, but usually only intracellular reversal in the more basal cells of the latter. In this case the susceptibility of the youngest hairs was often decreased below that of the oldest.

Staining in neutral red so dilute as to give a barely perceptible yellowish tinge to the water induced complete or nearly complete reversal in some of the youngest hairs, but only more or less reversal of intracellular gradients in the older. It was also

found that in some plants the gradients of the youngest hairs were almost completely reversed after two or three days in the laboratory and after a day or two more these hairs were dead.

Of course intermediate conditions between the normal and reversed gradient are frequently observed. In such conditions the intracellular gradient may be absent or very irregular and the hair gradient may be slight or even absent over a length of several cells. The differences in susceptibility between apical and basal end are, however, so great, particularly in the older hairs, that at the stage when the gradient is obliterated in one region of the hair other portions are either still normal, already reversed or dead.

Where the gradient is obliterated or reversed the hairs show a marked tendency to separate into their individual cells. Apparently the persistence of the orderly multicellular axis is associated with the persistence of the gradient. Other cases in which this separation appears will be described later.

The hairs of *Polysiphonia* are similar in structure and growth to those of *Chondria*, but in *P. variegata* and *P. fibrillosa*, the only species examined thus far, they are considerably more susceptible than the *Chondria* hairs and therefore not so favorable for experimental work. The gradient is primarily basipetal both in the hair in general and in the cell, and while more or less reversal has sometimes been observed, experimental reversal has not been attempted.

The hairs of *Griffithsia* differ from those of *Chondria* chiefly in the whorled arrangement of branches (Fig. 5) and as we should expect, since growth is primarily apical, both general and intracellular gradients are basipetal when the hair is in good condition. After two or three days in the laboratory, however, irregularities and reversals appear, and the hairs soon separate into cells or fall off entire.

DISCUSSION.

It is evident that at least the hairs of these three kinds among the algæ show axial susceptibility gradients like those in the vegetative axes of the thalli. Moreover, these gradients show a direct relation to the location of the vegetative point, the region

of highest susceptibility being in general the region of the vegetative point, at least when the hair is in good condition.

In *Fucus* and *Castagnea*, for example, where the vegetative point is basal, the gradient is normally acropetal, while in all other forms examined the vegetative point is apical and the gradient normally basipetal.

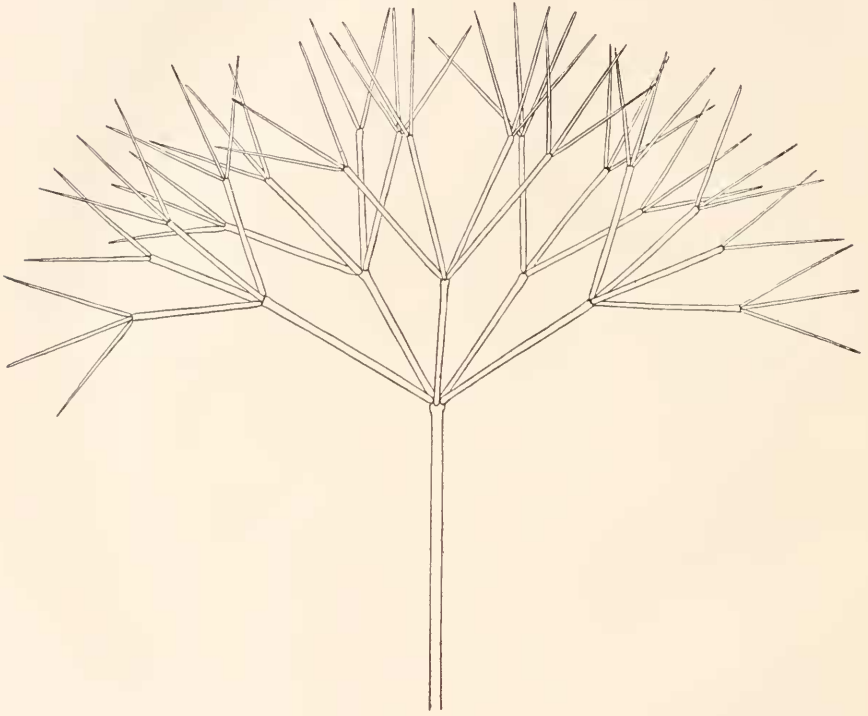


FIG. 5.

Under depressing conditions which are not extreme enough to kill rapidly the gradient may be more or less completely obliterated or even reversed, and such changes are of course a consequence of the differential susceptibility originally present. Obliteration or reversal of a gradient by external factors means simply that a region of highest susceptibility or metabolic rate, is affected by the external factor to so much greater extent than a region of lower susceptibility or rate that the original differences are obliterated or even reversed. In some cases an external

agent may reverse the susceptibility to itself, as in the case of neutral red, and it is also possible in many cases to determine the effect on susceptibility of one agent by using another for killing after exposing to the first. The whole complex problem of the nature of the action of external agents of different kinds on protoplasm is involved in these data on susceptibility, but even though we are far from the solution of that problem we can establish certain general laws of susceptibility as characteristic features of a physiological axis, *i. e.*, as an expression of polarity.

When the gradient is obliterated or reversed multicellular hairs often separate more or less completely into individual cells. The persistence of the hair as a multicellular order seems to be associated with the existence of the gradient. It will be shown elsewhere that this is true, not only for these hairs, but for the vegetative axes of certain species of algæ. Tobler ('02, '04) has observed in various species of the red algæ this tendency to separate into cells under unfavorable conditions and has used it as a method for inducing experimental reproduction. In the isolated cells of the hairs reproduction can scarcely be expected, but the relation between morphological order and physiological correlation is evident. After obliteration or reversal of the dynamic axial gradient the morphological order soon ceases to exist except where the structural stability is high.

A question of some interest concerning what may be called the death-level arises particularly in connection with the *Chondria* hairs. The young highly susceptible hairs of *Chondria* die without perceptible reversal of the gradient under conditions which bring about complete reversal in the hairs of medium age and some reversal of intracellular gradients with perhaps partial reversal of the hair-gradient in the oldest hairs. To reverse the gradient before death in the youngest hairs less extreme conditions must be used. These and various other facts suggest the possibility that the death-point, or more properly speaking, the death-level is not necessarily the same quantitatively for more active and less active protoplasm of the same kind and for more and less rapid killing, in other words the death-level may be relative rather than absolute. With our present lack of knowledge this remains merely a possibility.

This possibility has already been suggested in connection with certain observations on susceptibility in the lower animals (Child, '13, pp. 118-119) and it seems worth while to call attention to it in this connection. Actually the death-level, whether relative or absolute, must be a resultant of various component factors such as aggregate condition of colloids, permeability, rate of metabolism or of certain reactions, etc., and there can be little doubt that different agents and conditions act primarily or chiefly on different factors in this complex. But since these are factors in determining the behavior of a system, *i. e.*, are correlated, not independent, changes in one cannot proceed beyond a certain limit without inducing changes in the others. This being the case, the death-level as a quantitative level at which persistence of the system as a whole becomes impossible, must be for each particular case of death a more or less definite level or region of the curve which represents the quantitative changes in the activity of living protoplasm or its component factors. On the other hand, the previous condition of the system and the character and rate of action of the killing agent may play a rôle in determining this level in different cases. If this suggestion is correct, then regions or cells of different susceptibility in the hairs do not necessarily attain exactly the same condition at the point of death, and the condition in a particular cell or region may differ according as it is killed rapidly or slowly.

Since the hairs represent real physiological axes, similar to other plant axes the question of their physiological relation to other axes must be raised. Unquestionably the development of a hair axis is a form of reproduction in a protoplasm specialized in some way. As a reproductive process it must result from physiological isolation (Child, '11, '15*a*, Chap. IX., '15*b*, Chap. V.) and, as I have pointed out, physiological isolation and reproduction may occur, not only as the result of increase in size but also under depressing conditions in consequence of decreased dominance, *i. e.*, decrease or obliteration of a preëxisting axial gradient. Hairs frequently appear on young apparently vigorous plants, but they are often very characteristic of advanced vegetative stages or of plants which seem to be in poor condition. In *Agardhiella*, for example, I have frequently observed that parts

of the fronds bearing hairs show a lower susceptibility than other parts (Child, '16b). The hair is an axis arising from a cell of a previously existing axis. Like any other physiological axis it represents a metabolic gradient and originates as such a gradient in a cell which, though apparently specialized in certain respects is still capable of undergoing growth and division. In species where the hairs are not extremely sensitive to laboratory conditions it will probably be possible to control their occurrence and development by controlling the metabolic condition of the plant and in this way to learn something of their physiological relation as axes to the other axes of the plant.

SUMMARY.

1. The unbranched unicellular hairs of *Ceramium*, *Chondrus* and *Agardhiella*, the unbranched multicellular hairs of *Fucus* and *Castagnea* and the branched multicellular hairs of *Chondria*, *Poly-siphonia* and *Griffithsia* all show an axial gradient in susceptibility to various agents.

2. In the hairs of *Fucus* and *Castagnea* in which the vegetative point is basal the normal hair gradient is acropetal while in the other species where growth is primarily apical the gradient is basipetal, *i. e.*, in all cases the region of highest susceptibility is the region of the "growing tip."

3. Obliteration or the reversal of the susceptibility gradients has been observed or induced in the hairs of *Ceramium*, *Fucus*, *Castagnea* and *Chondria* and to some extent in those of *Griffithsia*. These changes in the gradient are dependent on the differential susceptibility to various depressing agents and conditions, which is a feature of the normal gradient. In general a high concentration or intensity kills so rapidly that reversal of the gradient cannot be demonstrated, but with lower concentrations or intensities the original differences in susceptibility may be obliterated or reversed before death occurs. In some cases a particular agent may reverse the susceptibility gradient to itself, and in others a reversal of the gradient produced by one agent may be demonstrated by the differential susceptibility to another.

4. The hair, like the vegetative portions of the plants, represents a physiological axis and the susceptibility gradient is one

aspect of the difference in metabolic and protoplasmic condition along the axis, in other words of the physiological polarity. The multicellular hairs often tend to separate into their cells when the gradient is obliterated or reversed, and the loss of the hairs under laboratory conditions or in other unfavorable environment is associated with the change in the gradient which usually occurs under such conditions.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO,
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